

PLANT SPECIES DIVERSITY AND CHEMICAL PROPERTIES OF SOILS IN THE CENTRAL DESERT OF BAJA CALIFORNIA, MEXICO

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A gradient in plant species diversity was investigated to determine how soil chemical properties limit the distribution of desert plants. Species-poor communities (lacking succulents) growing on basalt-derived soils were compared with richer communities on soils that developed on basalt or quartz diorite. Species richness and density were determined in three 100-m² quadrats at five sites. Soil samples were collected from A (0–10 cm) and B (10–30 cm) layers near the center of each quadrat. Leaves of species growing in or near quadrats were collected as indicator tissue. Elemental concentrations were measured in soil saturation extracts and leaf tissue digests. Surface soils were non-saline and had near-neutral pH. Soil saturation extracts were high in NaCl and adequate in Ca but low in N, P, B, K, Mg, S, and Fe. Leaves of indicator plants (*Viguiera* spp.) were high in K, Ca, and Na, medium in B, and low in Mg, P, and some micronutrients. Analysis of variance revealed that the Ca:Mg ratio in the soil solution differed significantly between sites and was lowest at species-rich sites. Simple regression revealed a moderate positive dependence of species richness on Mg in the soil solution and a negative dependence of species richness on soil solution Ca:Mg. But a marked dependence was found when species diversity (Shannon-Weiner *H'* Index) was regressed on Ca:Mg in the soil solution. These results indicate that the geographic ranges of desert species (and of succulents in particular) can be restricted by even moderate Ca in the rooting medium when Mg is critically low. Magnesium concentration in

leaves of species studied in Baja California was among the lowest, and Ca:Mg ratios among the highest ever reported in desert plants.

The species diversity of desert plant communities is commonly regulated by soil factors. Salt-tolerant (halophyte) and other "indicator" plants dominate the most extreme habitats, and glycophytes the more favorable (Fireman and Hayward 1952; Salinity Laboratory Staff 1954; Chapman 1975). In gradients of habitat severity, diversity (as well as growth and density) generally increases as the intensity of physiological stress decreases (Krebs 1972; Ungar 1974). The number of factors that regulate plant distribution also increases as habitat severity decreases.

While soil salinity and sodicity strongly influence the distribution and abundance of desert plants, the relative concentrations of the major cations (Na, K, Ca, and Mg) in the soil solution also play a significant role (Ayyad and El-Ghareeb 1972; Wallace et al. 1973; El-Ghareeb and Hassan 1989). Weak to moderate correlations have been reported between the concentration of individual cations in the soil solution and community attributes of desert plants, but higher correlation values resulted when cation ratios were considered instead (Ayyad and El-Ghareeb 1972; El-Ghareeb and Hassan 1989). In less severe environments, the availability of nutrient elements in the soil also can affect the composition of communities (Ayyad and El-Ghonemy 1976; El-Ghonemy et al. 1977).

Little information is available on how differences in chemical properties of soils affect the geographic distribution of plant species in the Sonoran Desert of Baja California. Moreover, little is known about how soil factors limit the distribution of native succulents (e.g., Nobel 1988). The purposes of this study were (i) to determine how chemical properties of soils and plant tissues vary along a gradient in soil parent material and species richness in the Central Desert of Baja California, (ii) to develop hypotheses on how these properties regulate the

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diversity of plant species, and (iii) to compare the concentrations and ratios of major cations in tissues of Baja California plant species with those of other dry regions of the world.

MATERIALS AND METHODS

Although the Central Desert of Baja California has long interested biogeographers and ecologists, little research has been done on its plant-soil relations. The region is presently subdivided into large ($> 100,000$ ha) communal land-holdings (ejidos) in which grazing of cattle is an important economic activity. We selected the study sites (Table 1) after observing a discontinuity in the vegetation that is characteristic of the area around Cataviña, Baja California. Soils that developed on quartz diorite parent material (i.e., La Virgen = LVN) support a rich Sonoran Desert perennial flora (Table 2) that consists of a shrub stratum (0–4 m) and an arboreal stratum that includes several stem succulents (4–20 m). On adjacent highlands to the south (Mesa El Gato; lower site = LMG, upper = UMG), basalt-derived soils support a low (mostly < 1 m), spe-

cies-poor vegetation. Further south (Laguna Chapala; N arm = NAL, NW arm = NWL), soils on basalt flows support richer communities that include occasional arborescent succulents (4–10 m).

Although the locations differ in altitude, the climate is similar across the 70-km distance between sites (Table 1). Across this region, an average of 40% of the precipitation falls in winter, 3% in spring, 21% in summer, and 36% in fall. Daytime temperatures often exceed 40°C in summer, but only a few sub-freezing nights occur in winter.

The study sites were selected on the basis of having representative vegetation and undisturbed soils (minimum erosion) that developed on an identifiable parent material. At each site, pits were dug to expose soil profiles, and soils were described and classified (Table 1) (Graham and Franco-Vizcaíno 1992). Perennial species were identified, and ground cover was measured in three 50-m transects by using the line-intercept technique (Table 2). The point of origin and direction of transects were selected at ran-

TABLE 1
Soil and plant sampling sites along a gradient in soil parent material and diversity of perennial plant species in the Central Desert of Baja California, Mexico

| Site (Abbreviation) | Location | Altitude (m) | Soil classification | Parent material | Landscape position | MAP ^a (mm) | MAT ^a (°C) | | |
|------------------------|-------------------------|-----------------|--|--------------------|------------------------------|--------------------------|--------------------------|--|--|
| Mesa El Gato | 114° 35' W 29° 35' N | 900 | fine, montmorillonitic, thermic, Petrocalcic Palear-gids | basalt | gently sloping ridge | 126 | 17.8 | | |
| | | | | | | | | | |
| | | | | | | | | | |
| Laguna Chapala | 114° 26' W 29° 23' N | 1000 | fine, montmorillonitic, thermic, Typic Natrargids | basalt | gently sloping ridge | | | | |
| | | | | | | | | | |
| | | | | | | | | | |
| La Virgen (LVN) | 114° 47' W 29° 49' N | 600 | mixed, thermic, shallow Typic Torripsamments | quartz diorite | nearly level slope amid tors | 116 | 18.8 | | |
| | | | | | | | | | |
| | | | | | | | | | |

^a Mean annual precipitation (MAP) and temperature (MAT) at weather stations at San Luis (Cataviña) and Laguna Chapala, División Hidrométrica, Secretaría de Agricultura y Recursos Hídricos and Grupo de Meteorología, CICESE, Ensenada, Baja California, Mexico.

TABLE 2

Species density, richness, and ground cover of perennial plants at five sites along a gradient in soil parent material and species diversity in the Central Desert of Baja California, Mexico

| Species | Basalt | | | Quartz Diorite LVN |
|--|--------------|--------------|---------------|-----------------------|
| | LMG | UMG | NAL | |
| <i>Density of succulent species^a, individuals/m²</i> | | | | |
| <i>Agave deserti</i> | NP | NP | NP | 0.06 ± 0.11 |
| <i>Agave cerulata</i> | NP | NP | 0.24 ± 0.03 | 0.33 ± 0.11 |
| <i>Echinocereus engelmannii</i> | NP | NP | 0.01 ± 0.01 | NP |
| <i>Ferocactus gracilis</i> | NP | NP | 0.007 ± 0.01 | 0.003 ± 0.005 |
| <i>Fouquieria columnaris</i> | NP | NP | P | P |
| <i>Lophocereus schottii</i> | NP | NP | P | 0.007 ± 0.006 |
| <i>Opuntia cholla</i> | NP | NP | 0.017 ± 0.006 | NP |
| <i>Opuntia molesta</i> | NP | NP | NP | P |
| <i>Pachycereus pringlei</i> | NP | NP | P | P |
| <i>Pachycormus discolor</i> | NP | NP | NP | P |
| <i>Density of non-succulent species^a, individuals/m²</i> | | | | |
| <i>Ambrosia camphorata</i> | NP | NP | 0.007 ± 0.01 | NP |
| <i>Ambrosia chenopodifolia</i> | 0.23 ± 0.3 | NP | P | 0.37 ± 0.19 |
| <i>Atriplex barclayana</i> | NP | NP | 0.057 ± 0.1 | NP |
| <i>Atriplex canescens</i> | NP | NP | 0.31 ± 0.05 | 0.003 ± 0.006 |
| <i>Atriplex polycarpa</i> | 0.007 ± 0.01 | NP | NP | 0.087 ± 0.05 |
| <i>Encelia</i> sp. 1 (<i>palmeri</i> ?) | 1.46 ± 0.57 | NP | NP | NP |
| <i>Encelia</i> sp. 2 | NP | NP | NP | 0.003 ± 0.006 |
| <i>Ephedra aspera</i> | NP | NP | 0.087 ± 0.15 | 0.037 ± 0.05 |
| <i>Eriogonum fasciculatum</i> | NP | NP | 0.04 ± 0.07 | 0.22 ± 0.18 |
| <i>Eriogonum scalare</i> | NP | NP | 0.21 ± 0.36 | 1.50 ± 0.70 |
| <i>Fouquieria splendens</i> | NP | NP | NP | 0.003 ± 0.006 |
| <i>Haplopappus propinquus</i> | NP | NP | NP | NP |
| <i>Krameria parvifolia</i> | NP | NP | NP | NP |
| <i>Larrea tridentata</i> | NP | NP | NP | 0.07 ± 0.03 |
| <i>Lycium</i> sp. 1 (<i>californicum</i> ?) | 0.32 ± 0.30 | 0.007 ± 0.01 | 0.007 ± 0.006 | 0.07 ± 0.08 |
| <i>Lycium</i> sp. 2 | 0.007 ± 0.01 | NP | NP | NP |
| <i>Prosopis glandulosa</i> | NP | NP | NP | P |
| <i>Simmondsia chinensis</i> | NP | NP | NP | 0.003 ± 0.006 |
| <i>Stipa speciosa</i> | NP | NP | NP | 0.01 ± 0.017 |
| <i>Viguiera deltoidea</i> | NP | NP | NP | P |
| <i>Viguiera purissimae</i> | P | 0.54 ± 0.37 | 1.07 ± 0.18 | 0.52 ± 0.30 |
| <i>Species richness, number^b</i> | | | | |
| 6 | 2 | 16 | 17 | 17 |
| <i>Ground cover %</i> | | | | |
| 31 ± 0.1 | 12 ± 4 | 26 ± 5 | 25 ± 6 | 23 ± 5 |

^a Average density ± SD, n = 3. "NP" denotes species not present at site (area within ~250 m of quadrats). "P" denotes species present at site but not found within quadrats.

^b Total number of perennial species at site.

^c Average cover % ± SD, n = 3.

dom, but were located within 50 m of the soil pits. Species diversity was determined by counting individuals growing within 1 m of the measuring tape (thus converting the transects into 100 m² quadrats) and calculating the Shannon-Wiener H' Index (Zar 1984) within each quad-

rat. We sampled plants and soils in October, and so species of *Encelia* and *Lycium* could not be distinguished because floral parts were lacking. Leaf samples (for use as indicator tissues) were bulked from several individuals of five species growing within or near quadrats. No single

species grew at all sites; thus it was necessary to use two species of the same genus for comparisons, and *Viguiera* was selected. The northern geographic limit of *Viguiera purissimae* is just north of Mesa El Gato, but *V. deltoidea* ranges into Alta California (Wiggins 1980). Leaf samples were washed in 0.1% Liqui-Nox detergent solution, rinsed thoroughly with distilled water, and dried in a forced-draft oven at 60°C. Tissues were ground to pass a #100 mesh, and 250-mg subsamples were digested in concentrated HNO₃ and HNO₃:HClO₄ (2:1) as in Ganje and Page (1974).

Soil samples were taken from the A (0–10 cm) and B (10–30 cm) layers near the center of each quadrat and from each horizon of the full profile exposed for description and classification. Soil samples were air-dried and passed through a 2-mm sieve. Saturated pastes were prepared with deionized water, and soil solution was extracted as in Rhoades (1982). The pH of the saturated pastes and the electrical conductivity of the saturation extracts (EC_e) were measured by using a pH meter (Model 811, Orion Research Inc., Boston MA) and conductivity meter (Model 34, Yellow Springs Instrument Co., Yellow Springs, OH). Soil saturation extracts and plant tissue digests were analyzed for Ca, Mg, Na, K, P, B, Fe, Mn, Cu, and Zn by using an inductively-coupled argon plasma spectrometer (Jarrell-Ash AtomComp Series 800 ICAP). Additionally, NO₃⁻-N, NH₄⁺-N, and SO₄²⁻-S were measured in saturation extracts by using a Technicon Auto Analyzer II (Technicon, Tarrytown, NY), and Cl⁻ was measured using a model 4425000 Chloridometer (Haake Buchler Instruments Inc., Saddle Brook, NJ). The chemical properties of the soil solution (i.e., saturation extract) in the rooting zone (0–30 cm) and in the entire soil profile (<1 m) were estimated by calculating averages weighted by the depth of individual layers (Bingham and Garber 1970). The relative level (low, medium, or high) of elemental concentrations in the soil solutions and plant tissues reported in the present study was determined by comparing them with published data for arable soils and unstressed crops producing standard yields. The concentrations of nutrient elements in "normal" crops were taken as: Ca 390, Mg 160, Na 95, K 90, P 115, B 10, Fe 2, Mn 1.5, Cu 0.16, and Zn 0.96 mmol kg⁻¹ dry weight (Gauch 1972). The median concentrations of elements in saturation extracts from 68 soil samples rep-

resenting 30 soil series in California were: Ca 1.5, Mg 0.5, Na 2, K 0.25, S 0.6, and Cl 0.7 mmol/L and B 9.25, Fe 0.5, Mn 0.2, Cu 0.5, and Zn 0.6 μmol/L (Bradford et al. 1971). Differences between sites in elemental concentrations in soil solutions and tissues were determined by one-way analysis of variance followed by Tukey's honestly significant difference test (Zar 1984). Linear regression was used to test for dependence of richness and diversity of perennial species on chemical properties of the soil, as well as for elemental concentration in tissues on concentrations in the soil solution.

RESULTS

Species richness (total number of species) and diversity (Shannon-Weiner *H'* index) were similar on soils on basalt at Laguna Chapala and on quartz diorite at La Virgen (Table 2, Fig. 1). But soils on basalt at Mesa El Gato supported communities poor in species (completely lacking in succulents) and with near-zero diversity (Fig. 1). Plant communities at both Laguna Chapala and La Virgen included succulent, halophytic and glycophytic species.

Soils were fine-textured on basalt and coarse-textured on quartz diorite (Table 1). The A and B soil layers (0–30 cm) were non-saline, and soil reaction ranged from slightly acid to slightly alkaline (Table 3). Soils are defined as saline if EC_e > 4 dS/m and sodic if the sodium adsorption ratio (SAR) of the saturation extract is > 13 mol/mol^{1/2} (Committee on Terminology 1987).

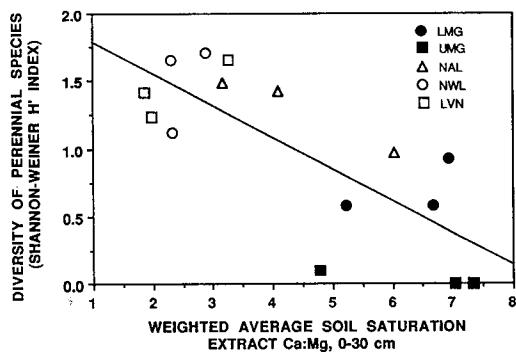


FIG. 1. Simple regression of species diversity (Shannon-Weiner *H'* index) on weighted average soil saturation extract Ca:Mg. $Y = 2.02 - 0.23 X$, $r^2 = 0.60$; $P < 0.001$. $H' = -\sum (p_i) (\ln p_i)$; where p_i is the proportion of all individuals of the *i*th species in the sample.

TABLE 3

Chemical properties of the soil solution along a gradient in parent material and plant species diversity in the Central Desert of Baja California, Mexico

| Chemical property | Basalt | | | | Quartz Diorite LVN |
|--|---------------|--------------|--------------|--------------|-----------------------|
| | LMG | UMG | NAL | NWL | |
| <i>Surface soil^a</i> <i>mmol/L</i> | | | | | |
| Ca | 1.21 ± 0.22 | 0.94 ± 0.19 | 1.49 ± 0.35 | 1.56 ± 0.91 | 0.79 ± 0.50 |
| Mg | 0.19 ± 0.03 | 0.16 ± 0.07 | 0.36 ± 0.14 | 0.65 ± 0.42 | 0.32 ± 0.12 |
| Na | 6.90 ± 6.66 | 5.33 ± 1.29 | 11.3 ± 1.14 | 20.6 ± 21.7 | 0.82 ± 0.19 |
| K | 0.11 ± 0.03 | 0.09 ± 0.02 | 0.24 ± 0.10 | 0.13 ± 0.06 | 0.17 ± 0.08 |
| N ^c | 0.17 ± 0.09a | 0.12 ± 0.05a | 0.10 ± 0.05a | 0.38 ± 0.13b | 0.44 ± 0.11b |
| S ^d | 0.30 ± 0.15 | 0.16 ± 0.05 | 0.21 ± 0.08 | 0.19 ± 0.07 | 0.09 ± 0.04 |
| Cl | 2.62 ± 3.33 | 0.85 ± 0.27 | 7.90 ± 2.73 | 13.5 ± 16.1 | 0.28 ± 0.04 |
| <i>μmol/L</i> | | | | | |
| P | 3.48 ± 0.59a | 3.63 ± 0.10a | 2.94 ± 1.04a | 2.05 ± 0.79a | 22.4 ± 7.91b |
| B | 9.42 ± 3.53ab | 15.9 ± 0.72c | 11.6 ± 2.67b | 17.3 ± 7.71c | 5.37 ± 2.98a |
| Fe | 0.14 ± 0.07 | 0.24 ± 0.07 | 0.14 ± 0.08 | 0.06 ± 0.07 | 0.09 ± 0.07 |
| Mn | 0.07 ± 0.01 | 0.07 ± 0.03 | 0.37 ± 0.43 | 0.07 ± 0.08 | 0.03 ± 0.01 |
| Cu | 0.67 ± 0.25 | 0.63 ± 0.11 | 0.45 ± 0.37 | 0.56 ± 0.14 | 0.47 ± 0.09 |
| Zn | 0.49 ± 0.40 | 0.12 ± 0.08 | 0.31 ± 0.04 | 0.26 ± 0.26 | 0.12 ± 0.09 |
| pH | 7.1 ± 0.1c | 6.3 ± 0.2a | 7.5 ± 0.1c | 6.9 ± 0.4bc | 6.8 ± 0.1b |
| EC | 0.8 ± 0.4 | 0.5 ± 0.05 | 1.4 ± 0.2 | 1.9 ± 1.8 | 0.3 ± 0.1 |
| SAR | 6.1 ± 6.1 | 5.2 ± 1.8 | 8.5 ± 1.9 | 12.4 ± 10.2 | 0.8 ± 0.1 |
| Ca:Mg ^e | 6.28 ± 0.92c | 6.38 ± 1.39c | 4.43 ± 1.45b | 2.51 ± 0.33a | 2.37 ± 0.78a |
| Na:K ^e | 60.2 ± 44.0 | 60.9 ± 18.6 | 56.4 ± 33.9 | 151 ± 139 | 5.32 ± 1.89 |
| <i>Soil profile^b</i> | | | | | |
| pH | 7.0 | 7.2 | 7.3 | 7.7 | 6.9 |
| EC | 3.9 | 2.5 | 14.3 | 4.4 | 0.2 |
| SAR | 43.3 | 20.5 | 27.8 | 29.7 | 1.6 |

^a Values for surface soil are means ± SD (*n* = 3) of weighted average (weighted by depth) chemical properties in soil saturation extracts of the A (0–10) and B (10–30 cm) soil layers. Means followed by a different letter are significantly different (*P* < 0.05) by the Tukey test.

^b Values for soil profiles (<1 m) are weighted averages of chemical properties of the entire profile (weighted by depth of individual horizons).

^c (NO₃⁻ + NH₄⁺)-N.

^d (SO₄²⁻)-S.

^e mol/mol.

The dominant cation in the soil solution at basalt sites was Na, but both Na and SAR were low at the quartz diorite site. The concentration of Na (and Cl) at LMG and NWL was highly variable, and this was reflected in the variability of the SAR. Charge balance and soil pH constraints (Salinity Laboratory Staff 1954) suggest that bicarbonates (which were not measured in the present study) were the dominant anions in the soil solution at Mesa El Gato, but Cl⁻ was dominant at Laguna Chapala.

The concentrations of N and S in the soil solution of the A and B layers were very low at

all sites (Reisenauer 1964; Bradford et al. 1971; Mengel and Kirkby 1982). Nitrate was the dominant species of N; the concentration of ammonium was of the order of 0.01 mmol/L in all extracts. Phosphorus was low at basalt sites, but medium at the quartz diorite site (Reisenauer 1964; Mengel and Kirkby 1982). The concentrations of Mg was lower than the median for California soils at all sites except NWL, and of K at all sites except NAL (Bradford et al. 1971). Calcium concentration was equal to the median for California soils at both NAL and NWL, but low at the other sites. Concentrations of B at

the basalt sites were about two orders of magnitude lower than the 10-ppm threshold for injury to tolerant crops (Bingham et al. 1970), but slightly lower at LVN. The concentrations of Cu at all sites were near the median, but those of Fe, Mn and Zn were generally lower than in California soils (Bingham et al. 1970; Bradford et al. 1971). Significant differences in soil reaction, in the concentrations of N, P, and B, and in the mole ratio of Ca:Mg in the soil solution were found between sites (Table 3). However, only the patterns of differences in N and Ca:Mg fit the pattern of species richness across the gradient studied.

Concentrations of Ca, Na, K, and B in leaves of *Viguiera* spp. (Table 4) were equal to or greater than those of "normal" crop plants (Gauch 1972). Concentrations of Ca in leaves were from 2.5 to 4.5, and of K from 3 to 7 times that in crops. At the basalt sites, Na concentrations were 2 to 3 times higher than in crops, but lower at LVN. At NWL, concentrations of B in leaves were 3 times higher than the average in crops, but near the average at the other sites. Magnesium was low at Mesa El Gato and NAL, but near the average at NWL and LVN. Only P and Fe were low in leaf tissues at all sites. Leaf concentrations of Mn, Cu, and Zn were low at some sites but not at others. Significant differences in concentrations of Mg, K, and Fe in leaf

tissue were found between sites, but only the pattern of increase in Mg concentration was the same as the pattern of increase in species richness. Neither the concentration Mg in the soil solution nor the ratios of Ca:Mg in plant tissues differed significantly between sites at the 5% level, but both parameters did differ significantly at the 10% level (unpublished data).

Simple regression disclosed moderate positive relationships between average Cu, Mg, and Ca:Mg in the soil solution and in leaf tissues of *Viguiera* spp. (Table 5). A moderate positive dependence of species richness on Mg in the soil solution was also revealed. But a stronger negative relationship between Ca:Mg in the soil solution and species richness was also found. However, when species diversity was considered instead of species richness, a marked dependence on Ca:Mg in the soil solution was revealed (Fig. 1).

Comparison of published average concentrations of major cations in leaves of species native to dry regions worldwide with those measured in the present work revealed that Mg content in the Baja California species studied was among the lowest, and Ca:Mg ratios among the highest ever reported (Figs. 2 and 3) (Garten 1976). The widest leaf Ca:Mg ratio recorded was that of *Viguiera purissimae* growing on basalt-derived soils (12.7 ± 3.8 , $n = 12$).

TABLE 4

*Elemental concentrations and mole ratios of major cations in leaves of *Viguiera* spp. along a gradient in soil parent material and plant species diversity in the Central Desert of Baja California, Mexico*

| Chemical property ^a | Basalt <i>Viguiera purissimae</i> | | | | Quartz Diorite <i>V. deltoidea</i> LNV |
|--------------------------------|--------------------------------------|---------------|-----------------------------|--------------|--|
| | LMG | UMG | NAL | NWL | |
| | | | <i>mmol kg⁻¹</i> | | |
| Ca | 970 ± 572 | 1287 ± 97.5 | 1359 ± 531 | 1762 ± 190 | 1063 ± 132 |
| Mg | 62.8 ± 18.9a | 114 ± 6.9c | 92.1 ± 6.24b | 177 ± 17.4d | 164 ± 4.19d |
| Na | 283 ± 227 | 216 ± 10.6 | 332 ± 125 | 256 ± 35.8 | 31.8 ± 17.3 |
| K | 307 ± 132a | 642 ± 9.22d | 601 ± 5.67d | 499 ± 65.2c | 402 ± 36.3b |
| P | 51.4 ± 5.98 | 57.1 ± 5.12 | 65.4 ± 8.91 | 67.6 ± 6.35 | 52.2 ± 12.3 |
| B | 16.2 ± 7.91 | 13.6 ± 0.51 | 15.2 ± 0.64 | 32.5 ± 11.1 | 11.1 ± 4.06 |
| Fe | 1.33 ± 0.07d | 0.72 ± 0.03ab | 0.72 ± 0.06a | 0.83 ± 0.09b | 0.96 ± 0.14c |
| Mn | 0.98 ± 0.41 | 1.11 ± 0.10 | 0.82 ± 0.14 | 0.62 ± 0.09 | 1.43 ± 0.49 |
| Cu | 0.21 ± 0.16 | 0.13 ± 0.05 | 0.14 ± 0.03 | 0.10 ± 0.06 | 0.09 ± 0.03 |
| Zn | 0.60 ± 0.28 | 0.59 ± 0.05 | 0.92 ± 0.20 | 0.70 ± 0.13 | 0.46 ± 0.26 |
| Ca:Mg ^b | 14.8 ± 5.7 | 11.4 ± 1.46 | 14.5 ± 4.61 | 9.98 ± 0.35 | 6.48 ± 0.77 |
| Na:K ^b | 1.43 ± 1.78 | 0.34 ± 0.02 | 0.55 ± 0.21 | 0.53 ± 0.15 | 0.08 ± 0.04 |

^a Values are averages ± SD, $n = 3$. Values followed by a different letter are significantly different ($P \leq 0.05$) by the Tukey test.

^b mol/mol.

TABLE 5

*Slopes of the regression lines (b) and coefficients of determination (r^2) for simple regressions of chemical properties in leaves of *Viguiera* spp. on chemical properties in the soil solution; and for species richness in quadrats on chemical properties in the soil solution*

| Chemical property in soil solution ^a | Chemical property in <i>Viguiera</i> spp. leaves ^b | | Species richness in quadrats ^c | |
|--|--|-------|---|--------|
| | b | r^2 | b | r^2 |
| Ca | 263 | 0.11 | 2.24 | 0.19 |
| Mg | 100 | 0.31* | 8.99 | 0.42** |
| Na | 4.66 | 0.12 | 0.13 | 0.17 |
| K | 231 | 0.02 | 21.1 | 0.21 |
| P | -562 | 0.24 | 87.1 | 0.04 |
| B | 476 | 0.08 | 4.79 | 0.00 |
| Fe | -537 | 0.04 | -15,700 | 0.15 |
| Mn | -310 | 0.03 | 5502 | 0.11 |
| Cu | 328 | 0.37* | -6237 | 0.07 |
| Zn | 364 | 0.13 | 547 | 0.00 |
| Ca:Mg | 1.28 | 0.36* | -1.21 | 0.48** |
| Na:K | 0.00 | 0.04 | -0.27 | 0.00 |
| (NO ₃ ⁻ + NH ₄ ⁺)-N | | | 0.09 | 0.18 |
| (SO ₄ ²⁻)-S | | | -0.42 | 0.02 |
| Cl ⁻ | | | 0.19 | 0.20 |
| SAR | | | 0.19 | 0.10 |
| EC | | | 1.72 | 0.21 |
| pH | | | -7.03 | 0.26 |

*.** Significant at the 0.05 and 0.01 probability levels, respectively. Total $df = 14$.

^a Depth-weighted (0–30 cm) average properties in saturation extract or paste (pH).

^b Leaf samples bulked from several individuals in or near quadrats.

^c Number of perennial species in 100-m² quadrats.

DISCUSSION

Soil-Plant Relations on Quartz Diorite and Basalt Soil Parent Materials

The soil solution in surface horizons at the sites studied was low in N, P, K, Mg, S, and Fe. The supply of dissolved N may increase during the wet season when biological activity is high, but the solubility of P and Fe is regulated by the characteristics of the solid phase (Mengel and Kirkby 1982). The concentrations of K, Mg, and S were low in the solution of the upper soil layers, but were generally higher in that of the deeper horizons (unpublished data).

While the upper 30 cm of the soils studied at basalt sites were non-saline, deeper horizons were sodic and non-saline at Mesa El Gato, and both saline and sodic at Laguna Chapala (Table 3). Soil pH at depths greater than 30 cm on the basalt sites ranged from neutral to strongly alkaline, and both pH and EC_e consistently increased with depth and corresponding increasing concentrations of Na. But on soils derived

from quartz diorite at La Virgen, EC_e was very low, and was highest at the surface and decreased with depth. The entire soil profile (rock contact occurred at 30 cm) was slightly alkaline, and pH varied only slightly.

Plants respond to average soil salinity of the entire root zone, but water absorption (and growth) is limited by salinity encountered by the least saline portion of the root system (Shahhev et al. 1968; Bingham and Garber 1970). Salinity both in the surface and subsurface soil was much higher at the species-rich sites at Laguna Chapala than at the much poorer sites at Mesa El Gato (Table 3). Observations in soil pits at all four basalt sites revealed few, very fine (<1 mm) roots at depths >30–40 cm; but fine (1–2 mm) and medium (2–5 mm) roots were common at depths <30 cm. Succulents are characteristically shallow rooted (Jordan and Nobel 1984) and presumably unaffected by subsurface salinity. This is confirmed by the occurrence of a number of succulent species at Laguna Chapala.

Although salinity in the soil solution of the A and B layers was insufficient to limit plant growth at the basalt sites studied, subsurface salinity may preclude the establishment of deep-rooted glycophytes. For example, salinity in C horizons can limit the distribution of *Larrea* (Salinity Laboratory Staff 1954; Wallace et al. 1973). Halophytes (e.g., *Atriplex*, *Lycium*) and salinity-tolerant glycophytes (e.g., *Prosopis*, *Simmondsia*) occur at Laguna Chapala, but *Larrea* does not (Table 2). All this suggests that, although salt stress averaged over the entire soil profile may be an important limiting factor at the Laguna Chapala sites, it is not severe enough in the upper soil profile to limit plant establishment. Thus, the absence of succulents and sa-

linity-tolerant glycophytes at Mesa El Gato suggests that their distribution is instead limited by another factor, possibly a nutritional imbalance.

Leaves of *Viguiera* spp. accumulated high concentrations of K, Ca, and Na, but were low in Mg (Table 4). The order of concentrations of major cations in the soil solution of the rooting zone at the basalt sites was Na >> Ca > Mg > K, and the order was Na = Ca > Mg > K at LVN. However, the order in leaf tissues of *Viguiera purissimae* at the basalt sites was Ca >> K > Na > Mg, and Ca >> K > Mg > Na in leaves of *V. deltoidea* at LVN. The pattern of high accumulations of Ca and K and restriction of Na from leaf tissues was similar for both

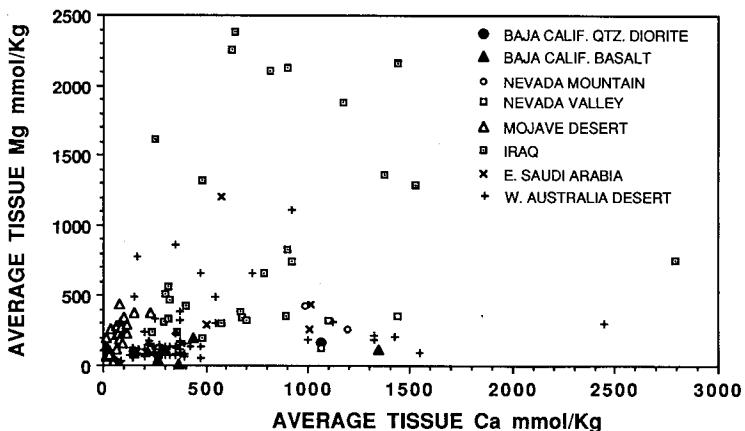


FIG. 2. Average concentrations of Ca and Mg in tissues of desert plants from Baja California, Mexico (this study), California, and Nevada, U.S.A. (Wallace et al. 1973), Iraq (Al-Ani et al. 1971), eastern Saudi Arabia (Al-Homaid et al. 1990), and West Australia (Keay and Bettenay 1969). Many data points represent only a single observation. Baja California species sampled in this study were (in order of increasing Ca), quartz diorite: *Ambrosia chenopodifolia* ($n = 3$), *Viguiera deltoidea* ($n = 3$); basalt: *Atriplex polycarpa* ($n = 5$), *A. canescens* ($n = 5$), *Ambrosia chenopodifolia* ($n = 8$), and *V. purissimae* ($n = 12$).

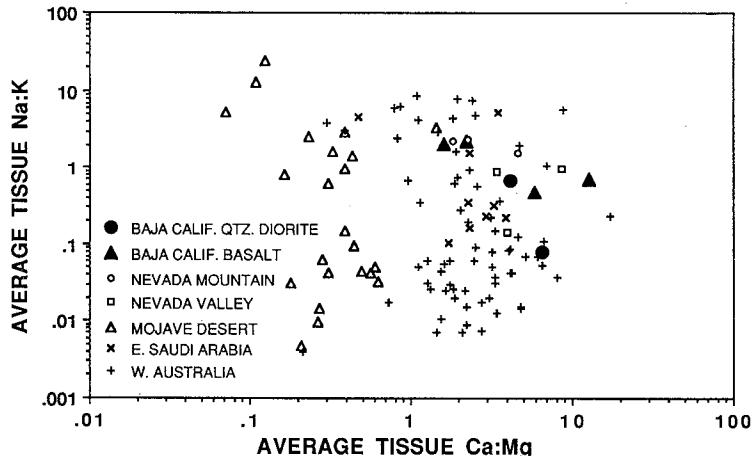


FIG. 3. Mole ratios of major cations in tissues of desert plants from Baja California, Mexico (this study), California, and Nevada, U.S.A. (Wallace et al. 1973), eastern Saudi Arabia (Al-Homaid et al. 1990), and West Australia (Keay and Bettenay 1969).

species, although *V. deltoidea* was growing in soil low in Na at LVN. It is important to note that Ca was not high in the soil solution across the gradient, but only low to medium. High concentrations of Ca in the soil solution can induce the expression of Mg deficiency (Embleton 1966). The large accumulation of Ca in leaves may therefore result from the plant compensating for low Mg in the soil solution. Evidence for this is provided by the much higher Ca:Mg ratios in tissues than in soil solution (Tables 3 and 4). An indication of Na restriction is provided by the marked difference in Na:K ratios in the soil solution compared with that in leaves.

Concentrations of B in leaves of *Viguiera* sp. were only 1 to 3 times that in leaves of "normal" crops. This suggests that B is also restricted from leaf tissues. Phosphorus in leaves was low at all sites, but was low in the soil solution only at basalt sites. A possible explanation is that the method used measures total dissolved P, but only a fraction of that may be available to plants at the observed soil pH (Mengel and Kirkby 1982). Micronutrient concentrations in leaves were low at most sites and only approached sufficiency in a few instances, but without an obvious pattern.

Thus, the suite of adaptations of *Viguiera* spp. to nutrient imbalance along the gradient studied appeared to be restricted accumulation of toxic elements (Na, B) while favoring the accumulation of useful (K, Ca) nutrients and tolerance of combined macro- and micronutrient deficiencies. An indication of the intensity of physiological stress posed by the soil solution of the gradient studied may be that, aside from *Viguiera*, no genus was common to more than four sites.

Magnesium in the soil solution was low at all sites, but ranged from low to medium in tissues (Tables 3 and 4); and regression analysis disclosed a moderate positive relationship between Mg in soil solution and plant tissues (Table 5). Thus Mg concentration in the soil solution may be limiting to plant growth. A similar relationship was found between Cu in soils and tissues, but Cu in the soil solution was near the median for California soils, and tissue concentrations were nearer the level in "normal" crops than that of Mg. The pattern of increase in Cu concentration in tissues was opposite that of the gradient in species richness. However, species

richness was highest at the sites where Mg content in tissues was highest (Tables 2 and 5).

The positive relationship between Ca:Mg in the soil solution and in leaf tissues (Table 5) suggests that the distribution of plants is limited not only by Mg deficiency, but also by competition for uptake between Ca and Mg where Mg is critically low. Although concentrations of Ca were moderate, Mg concentrations were sufficiently low to result in high Ca:Mg ratios. These results suggest that Mg deficiency, enhanced by high Ca:Mg ratios in the soil solution, may result in reduced species richness across the gradient studied (Table 5). Barrens typically result from nutrient imbalances in the soil (especially major cations) or from toxic concentrations of non-nutrient elements (Daubenmire 1974). A marked dependence was found when species diversity measured in quadrats was regressed on average Ca:Mg in the soil solution (Fig. 1). The transition between glycophytic and tolerant vegetation occurred at Ca:Mg ~4; soils at NAL appeared to bridge the gap in Ca:Mg ratios.

Soil physical properties such as texture appear to have little influence on the distribution of halophytes on salt-affected soils (Mitchell et al. 1966), but textural differences may result in differences in the water relations of plants. Water infiltrates into coarse textured soils more rapidly, and coarse textured soils hold water less tightly than fine textured soils. Additionally, surface crusts may form on fine textured soils that impede water entry and expose it to evaporation. Differences in soil texture as well as the marked sodicity of deeper soil horizons in basalt-derived soils may also have been important factors in limiting the distribution of plants in the gradient studied. The combination of higher matric and osmotic components of water potential in basalt soils may make water significantly less available than in soils on quartz diorite. Such soil factors may also account for the observed differences in the abundance and height of arborescent succulents between soils on quartz diorite and basalt parent materials.

Magnesium concentrations in leaves analyzed were low enough to pose a potential hazard of hypomagnesemia for grazing cattle. Grass tetany can occur when cattle feed on native vegetation growing on calcareous soils low in Mg, but the relationship between soil properties and the incidence of tetany is equivocal (Reid and Horvath 1980). Hypomagnesemia is not caused

by poor forage, and is more likely to occur during periods of cool, wet weather in ruminants on high forage regimens (Fontenot 1972). Grass tetany has not been reported, nor are environmental factors favorable for its occurrence in the Central Desert of Baja California.

Global Comparison of Content of Major Cations in Leaves of Desert Plants

Comparison of published average cation contents in leaves of desert plants worldwide with those analyzed in the present study revealed that many desert plants accumulate high concentrations of both Ca and Mg, but some are low in both cations (Fig. 2). Tissues from some species analyzed in the present study were low in both cations, but Mg in two species from the basalt sites was among the lowest concentrations recorded. Slightly higher Mg concentrations were recorded for species growing on basalt- and quartz diorite-derived soils that accumulated excess Ca. Low Mg concentrations have also been reported in the soil solution and tissues of native *Simmondsia chinensis* in Baja California (Franco-Vizcaíno and Khattak 1990).

Wallace et al. (1973) reported cation contents in leaves of Mojave Desert species and along a gradient in salinity (also inhabited by *Lycium* spp.) from a mountain to a saline valley in the Basin and Range province in Nevada. Mojave Desert species were low in Ca and ranged from low to high in Mg (Fig. 2). Plants along the mountain-to-valley salinity gradient showed similar concentrations of Ca, but higher Mg than the species reported in the present study. Iraqi species were generally richer in Mg than species from North America, West Australia, and eastern Saudi Arabia (Keay and Bettenay 1969; Al-Ani et al. 1971; Wallace et al. 1973; Al-Homaid et al. 1990). Concentrations of Ca and Mg in leaves of some Australian species were similar to those reported for the salinity gradients in Nevada and in the present study (Fig. 2).

Plants tolerate salinity by controlling salt uptake by roots and by compartmentalizing salts in leaves (Osmond et al. 1987). Hence, the chemical composition of plant tissues varies from site to site, but it has been suggested that elemental ratios may be relatively unaffected by geographic variation (Garten 1976). We show that tissue cation ratios occur in clusters that may be indicative of regional differences in cation

availability (Fig. 3). Ratios of Ca:Mg were mostly <0.8 for Mojave Desert plants but mostly >1 for West Australian species. Numerous surface exposures of minerals rich in Mg occur in the Mojave Desert (California Division of Mines and Geology 1950), but West Australian soils were reported low in Mg (Keay and Bettenay 1969).

The cluster of cation ratios in species from the salinity gradient in Baja California was largely superimposed on that of the gradient in Nevada (Fig. 3). In both gradients, Ca:Mg was greater at the more saline (basalt or valley) sites. Ranges of ratios of major cations in leaves of Baja California and Nevada species growing in salinity gradients were entirely within the ranges of West Australian and Saudi Arabian plants. This may indicate similarities in the supply of cations in the soil solution of the three regions.

Iraqi species are low in K (for which data are not available) and Ca, but rich in Na and Mg (Al-Ani et al. 1971); they probably occupy the upper left quadrant in Fig. 3. The pattern of accumulation of major cations in plants growing in serpentine soils is likely to be similar to that of plants from the Mojave and Iraqi deserts and opposite that of Baja California, Nevada, and West Australia. Thus, analysis of cation ratios in plant tissues may be used to indicate and compare the limitations posed by the imbalance of cations in the soil solution and to classify patterns of cation accumulation by plants.

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